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ORIGINAL PAPER

Heterozoan carbonates in subtropical to tropical settings in the present and past

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Abstract Water temperature has received considerable attention as steering factor for the genesis of different types of marine carbonate sediments. However, parameters other than temperature also strongly influence ecosystems and, consequently, the carbonate grain associations in the resulting carbonate rock. Among those factors are biological evolution, water energy, substrate, water chemistry, light penetration, trophic conditions, CO_2 concentrations, and Mg/Ca ratios in the seawater. Increased nutrient levels in warm-water settings, for example, lead to heterotrophic-dominated associations that are characteristic of temperate to cool-water carbonates. Failure to recognize the influence of such environmental factors that shift the grain associations towards heterotrophic communities in low latitudes can lead to misinterpretation of climatic conditions in the past. Modern analogues of low-latitude heterozoan carbonates help to recognize and understand past occurrences of heterozoan warm-water carbonates. Careful analysis of such sediments therefore is required in order to achieve robust reconstructions of past climate.

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Introduction: carbonate sediments as environmental archives

The increasing public focus on climatic and global changes makes reliable environmental reconstructions of the past more crucial than ever. The record of the past is an important basis for understanding the processes, interactions and dynamics of changing environmental conditions. The short-term changes we observe today are but snap shots. Hence, for extrapolating current trends, for assessing causes, dynamics, and reaction strategies, a deep-time perspective is extremely valuable. Sedimentary rocks are the most important archives of environmental conditions during Earth history. Among sedimentary rocks, carbonates are particularly valuable, because they are mostly of biogenic origin and thus record environmental conditions with a wealth of different facets.

Until the end of the 1960s, it was generally accepted that the formation of volumetrically significant carbonate deposits is restricted to the tropical-subtropical climate belt. In fact, the approach to study modern systems as analogues for ancient deposits was developed in warm-water settings (Ginsburg 1956, 1957; Purdy 1961, 1963). It was only in the late 1960s when it was recognized that significant carbonate production also takes place outside the tropics in settings where terrigenous influx is restricted (Chave 1967). Generally, the region of tropical carbonate sedimentation is separated from extra-tropical regions of carbonate formation by the 20°C winter isotherm

(e.g., Betzler et al. 1997); however, the distribution of modern coral reefs is constrained by winter minimum temperatures above 18°C (Newell 1971; Belasky 1996). In the 1980s, numerous studies have dealt with modern extra-tropical carbonates, in particular in the southern hemisphere (Nelson et al. 1988; James and Bone 1989; James et al. 1992; James 1997). During the 1990s, numerous studies focused on carbonate settings of polar regions (Henrich et al. 1992, 1997; Andruleit et al. 1996; Freiwald 1998; Rao et al. 1998). Modern deep-water carbonates came into focus with improved marine technology, and since the late 1990s, intensive research of benthic deep-water carbonates such as coral mounds takes place (see reviews of Roberts et al. 2006, 2009).

The approach to study modern analogues has greatly improved the interpretation of ancient carbonate rocks (e.g., Grammer et al. 2004). Studies of modern carbonate depositional systems establish relationships between external parameters that, in contrast to the geological past, can be directly measured (cf. Westphal et al. 2010). This includes oceanographic parameters such as seasonality, trophic conditions, temperature, and salinity (Lees and Buller 1972; Carannante et al. 1988). In contrast, studies of ancient carbonate systems have traditionally focused on the interpretation of temperature and relative sea-level position (e.g., Kendall and Schlager 1981; Handford and Loucks 1993). More recent studies of ancient carbonates emphasize the influence of trophic conditions and ocean chemistry among other factors (Pomar 2001a; Hallock 2001; Pomar et al. 2004).

While the actualistic concept of the three large carbonate realms (warm, cold, deep) is by now well established (see Schlager 2003), the large and diverse group of carbonates that do not fit into this scheme is currently strongly under-represented in the literature. Wright and Burgess (2005) developed the concept of a carbonate production continuum in order to include the latter. Carbonate sediments that do not fit into the traditionally recognized realms appear atypical from the actualistic point of view; for example, heterotrophic-dominated carbonate sediments in warm-water low-latitude settings are rare in the modern world. However, associations that are unusual today might have been typical during intervals of Earth history when different environmental boundary conditions or different biotic strategies prevailed.

Only isolated modern examples of such "atypical" carbonates have been studied in detail so far. Thus, comparison to and interpretation of ancient occurrences remain difficult. The recognition of such carbonates, however, is of utmost importance for paleoclimate research. For example, misinterpretation of fossil carbonates formed in the tropics under elevated nutrient conditions as cool-water carbonates would lead to wrong paleoclimatic reconstructions that might ultimately be used as input for climate modelling. For achieving reliable climatic and environmental reconstructions, the differentiation of the various environmental influences is required. Classical carbonate sedimentological tools for the definition of carbonate facies and carbonate grain associations can be inadequate if the spectrum of external influences is not included in the interpretation (e.g., hydrography, productivity), as well as the biological reactions to environmental change in time and space (physiological adaptation, shifts in the species spectra; e.g., Henrich et al. 1995). An understanding of the carbonate depositional systems is also important for reservoir rock characterization. Architecture, ecological accommodation, facies distribution and diagenetic potential sensibly react to changes of the biological community (Pomar 2001a, b; Knörich and Mutti 2006).

In spite of the increasing recognition of influences beyond temperature, the literature is still dominated by temperature or paleolatitude interpretations of carbonate grain associations. One reason is that a concept of heterozoan and transitional photozoan-heterozoan (cf. Halfar et al. 2006) carbonates in warm-water low-latitude settings has not yet been formally established. The aim of this paper is therefore to provide an overview of these heterozoan warm-water carbonates and the control mechanisms leading to their specific composition.

Carbonate grain associations as climate and latitudinal indicators

Classical tropical carbonates are largely produced by autotrophic and mixotrophic biota such as zooxanthellate corals and calcareous green algae. They are restricted to oligotrophic waters, because the strategy of photosymbiosis and internal recycling is most successful under nutrient-limited conditions (Hallock 1981; Wood 1993). Also, photoautotrophic organisms are adapted to low nutrient levels and are suppressed in high-nutrient settings (Hallock and Schlager 1986; Hallock 1987; Schlager 2003).

In the modern world, carbonate sediments that are mainly produced by heterotrophic organisms are dominant in temperate to polar regions (see James 1997). However, they also occur in the tropics where the oceanographic situation suppresses typical tropical chlorozoan carbonates (Logan et al. 1969; Simone and Carannante 1988; Hallock et al. 1988; Carannante et al. 1988). Controls that influence the formation of heterozoan versus chlorozoan carbonates in the tropics include temperature, salinity, water depth, trophic conditions, oxygen and CO_2 concentrations and Mg/Ca ratio in the seawater, alkalinity, morphology and bathymetry of the sea-floor, the type of substrate, transparency of the water column, internal waves and water

stratification (Hallock and Schlager 1986; Hallock et al. 1988; Carannante et al. 1988; Bourrouilh-Le Jan and Hottinger 1988; Stanley and Hardie 1998; Pomar and Ward 1995, 1999; Pomar 2001a; Mutti and Hallock 2003; Pomar et al. 2004; Wright and Burgess 2005). Some of these conditions are strongly influenced by coupled atmospheric and oceanographic circulation patterns. For example, trade wind cells and the stable subtropical gyres of the Atlantic and Pacific Oceans cause upwelling preferably along the western sides of continents; the formation of the near-equatorial oceanic upwelling belt follows the Intertropical Convergence Zone. Other factors, such as eustacy, tectonics, and sea-floor morphology determine the accommodation space, the extension and the morphology of the carbonate factory (e.g., Handford and Loucks 1993; Reijmer et al. 1992). Trophic conditions, temperature, and water energy determine the biotic associations (e.g., Hallock and Schlager 1986). Type and location of the carbonate production determine the base level of sediment accumulation and thus the platform morphology and dynamics (Pomar 2001b).

Lees and Buller (1972) and Lees (1975) already emphasized that modern foramol sediments are not restricted to extratropical areas but occur also in the tropics and subtropics (Fig. 1). Similarly, James (1997) pointed out that while cool-water carbonates are always heterozoan carbonates, the heterozoan association is not indicative of cool-water carbonates. An exception is the distribution of phototrophic calcareous red algae. These Corallinaceae differ from typical chlorozoan elements in that they tolerate

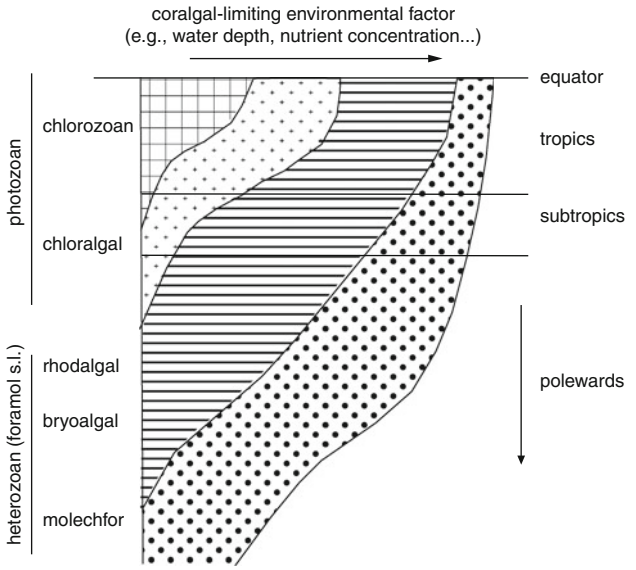

Fig. 1 Latitudinal distribution of carbonate facies as a function of water depth modified from Carannante et al. (1988). The *axis* indicating increasing water depth (and thus decreasing water temperature and light) in the original figure here also serves for other parameters such as increasing nutrient concentrations

higher nutrient levels than other phototrophic or symbiotic organisms, and their genera are adapted to temperatures that span from tropical to polar conditions (e.g., Freiwald 1998).

The influence of trophic conditions has been increasingly recognized in carbonate sedimentology over the past decades (Hallock and Schlager 1986; Carannante et al. 1988; Birkeland 1987; Hallock 1988, 2001; Pomar et al. 2004). The most important biolimiting nutrients for carbonate depositional systems are phosphorous, iron, silica and nitrogen (Brasier 1995a). Nutrients can be introduced into the sedimentary system by several processes including oceanic upwelling, fluvial transport, wind transport and volcanic eruptions (Vogt 1989; Mutti and Hallock 2003; J. Michel, G. Mateu-Vicens, H. Westphal, 2010, Eutrophic tropical carbonate grain associations—the Golfe d'Arguin, Mauritania, submitted). Changes in trophic conditions result in shifts in the diversity, composition, trophic structure and stability of the biological community (Valentine 1971; Stanton and Dodd 1976, Brasier 1995a, b).

The systematic paleoecological interpretation of ancient carbonate rocks usually applies the characterization of grain associations, that is, the characteristic combinations of remains of carbonate secreting organisms (Lees 1975). The coralgal association is composed of skeletal remains of corals and green algae; the chloralgal association is dominated by green algae. Together they are typical for oligotrophic tropical conditions (Lees and Buller 1972) and correspond to the chlorozoan group (James 1997). Foramol (Lees and Buller 1972), rhodalgal and molechfor (Carannante et al. 1988), bryomol (Nelson et al. 1988), and bryohyalosponge (Beauchamp 1994) associations correspond to the heterozoan group of James (1997) and are well known from the extra-tropics. Henrich et al. (1995) have shown in studies of arctic and subarctic carbonates that a distinction between tropical and arctic carbonates simply on the basis of component associations is impossible. They conclude that the interpretation of grain associations is insufficient without considering the trophic conditions and without including knowledge of the biogeographical affinities of genera or species involved in carbonate sedimentation. This can be exemplified by the cosmopolitan group of coralline algae. While today Sporolithaceae are characteristic of low latitude, mainly deep-water settings, melobesioid corallinaceans occur also in high latitude, shallow-water settings, whereas lithophylloid and mastophoroid corallinaceans are characteristic of mid to low latitudinal shallow waters (Aguirre et al. 2000). Hence, the incorporation of taxonomic knowledge to carbonate-grain association promises a very valuable source of information but this often remains unrecognized in sedimentological studies.

Biological evolution, however, limits the applicability of modern grain associations as analogues for interpreting past latitudinal position or paleotemperatures. For example,

Carannante et al. (1995) have shown that in certain stratigraphic intervals, foramol associations have even dominated the tropics, as for example in Upper Cretaceous rudist bearing limestones, which have formed in the tropics. Therefore, caution is required when interpreting ancient carbonate grain associations in terms of latitudes or temperatures without considering taxonomic evidence and other environmental parameters.

Modern heterozoan warm-water carbonates

In contrast to oligotrophic tropical carbonate depositional systems, modern heterozoan tropical carbonates are comparably rare. Generally, temperature and nutrient levels are anticorrelated in modern oceans (e.g., Halfar et al. 2006). In settings with enhanced fluvial input, increased nutrient levels are generally accompanied by a decrease in salinities and an increase in sediment load. However, there are few examples where cool upwelling waters warm up on broad shallow tropical shelves while staying saline and meso- and eutrophic. Such examples allow for singling out the effects of trophic conditions.

In the following, modern heterozoan warm-water carbonate depositional systems are described. Study of modern systems has the great advantage that environmental parameters can be directly measured, allowing for linking sediment parameters to environmental (oceanographic, ecologic) conditions. Therefore, modern analogue studies are a crucial step for understanding heterotrophic warm-water carbonates in the rock record. The following modern occurrences of warm-water heterozoan carbonates are categorized according to the dominant steering mechanisms (Figs. 2, 3).

Trophic conditions

Nutrients can stimulate growth of phytoplankton that reduces water transparency, limiting depth ranges of zooxanthellate corals and calcareous algae, and thereby reducing phototrophic carbonate production (Hallock and Schlager 1986). Hence, if nutrient and food resources are plentiful, small fast growing groups including filamentous algae, barnacles, and bryozoans among others are superior competitors for space to corals (Birkeland 1987). A modest increase in nutrient flux causes a shift from coral to mixed coral-algal domination, and a substantial increase in nutrient flux produces a shift from coral to filter-feeding domination with non-symbiotic and heterotrophic biota (Hallock 2001).

NW-African shelf of Northern Mauritania

The generally narrow continental shelf of most parts of NW-Africa (<65 km) widens off N-Mauritania to some 150 km at the Golfe d'Arguin. This extensive gulf hosts the shallow Banc d'Arguin with water depths of less than 10 and in many areas less than 1 m. The waters off N-Mauritania are among the most productive marine areas (3 mg * m^{-3} Chl-a (chlorophyll-a), e. g., Marañón and

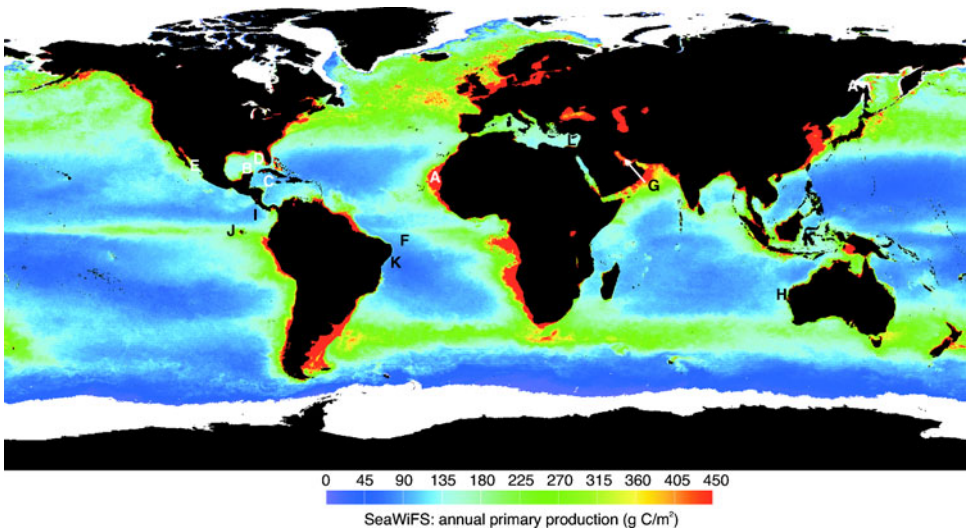

Fig. 2 Location of modern heterozoan warm-water carbonates discussed in text. *White letters* indicate high-nutrient setting; *black letters* indicate settings where factors other than trophic conditions suppress typical tropical photozoan communities. (*A*) Mauritania; (*B*) Yucatan; (*C*) Nicaragua Rise; (*D*) West Florida Shelf; (*E*) Gulf of California; (*F*) Fernando de Noronha; (*G*) Persian Gulf; (*H*) Shark Bay, W-Australia; (*I*) Cocos Island; (*J*) Galapagos Islands; (*K*) NE Brazilian shelf; (*L*) Eastern Mediterranean. Map shows primary production based on chlorophyll concentrations (annual average, September 1997—August 1998) (http://marine.rutgers.edu/opp/swf/Production/results/all2_swf.html)

Holligan 1999) in the world and are important fishing grounds. The reason for the high productivity lies in the elevated nutrient levels caused by oceanic upwelling and by additional fertilization by high desert dust input. Cold oceanic upwelling along the NW African coastline stretches from 12°N to 33°N (Mittelstaedt 1991; Van Camp et al. 1991) and gives rise to the formation of cool-water carbonates that dominate most of this region (Summerhayes et al. 1976). An exception is the Golfe d'Arguin, where the upwelling waters warm up to subtropical-tropical temperatures that on the Banc d'Arguin can exceed 25°C in summer and do not drop below 18°C in winter; where the upwelling waters enter the bank, minimum temperatures are at 16°C (Peters 1976, Koopmann et al. 1979). At the same time trophic levels remain high, thus producing eutrophic warm-water conditions.

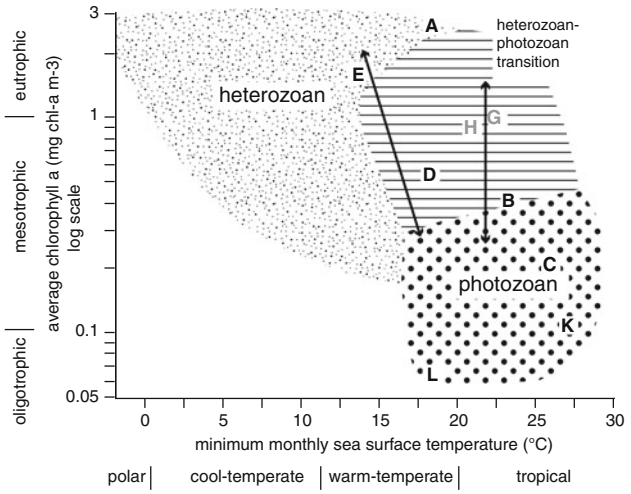

Fig. 3 Nutrient-temperature scheme modified after Halfar et al. (2006). Examples discussed in text are indicated (where chlorophyll-a values were available) with *letters* as in Fig. 3. The geographical gradients of (*E*) and (*G*) are indicated by *arrows*. Note that several examples discussed in text plot in the photozoan field; these are the examples where steering factors other than nutrients and temperature suppress the development of a photozoan community. The plot was originally designed for normal-marine salinities; examples with elevated salinities therefore here are marked by *grey letters*. Temperature and chlorophyll values are from Halfar et al. (2006) or from description of examples in text

In the shallow northern part of the Golfe d'Arguin, the Baie du Lévrier, the elevated nutrient levels result in a sediment grain association composed of barnacles, worm tubes, red algae, bryozoans, and alcyonarians; in settings below the wave base, ostracods, foraminifers, echinoderms, sponge spicules, diatoms and fish remains prevail (Koopmann et al. 1979). The originally cold temperature of the upwelling waters is documented by cool-water planktonic foraminifers such as *Neogloboquadrina pachyderma* that are transported onto the bank and into the bay (Koopmann et al. 1979; J. Michel, G. Mateu-Vicens, H. Westphal, 2010, Eutrophic tropical carbonate grain associations—the Golfe d'Arguin, Mauritania, submitted).

South of the Baie du Lévrier the sediment is dominated by bivalves with abundant fish remains and serpulid tubes (Fig. 4a; J. Michel, G. Mateu-Vicens, H. Westphal, 2010, Eutrophic tropical carbonate grain associations—the Golfe d'Arguin, Mauritania, submitted). Organisms typical of oligotrophic tropical settings (e.g., zooxanthellate corals and green algae) are absent. The species spectrum of the molluscs is very narrow as typical for high-nutrient

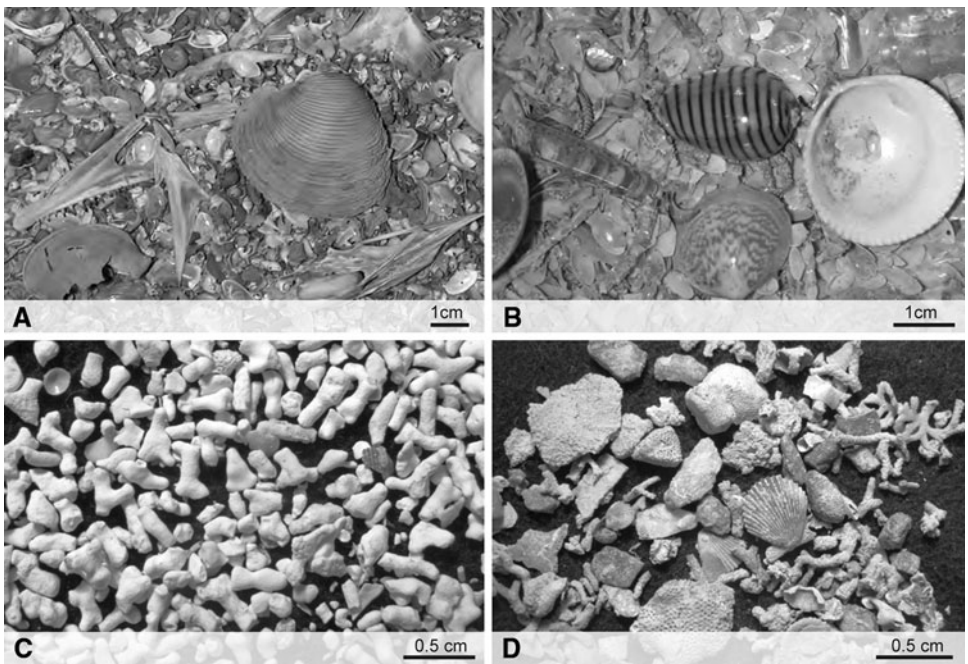

Fig. 4 Examples of modern heterozoan warm-water carbonate grain associations: **a**, **b** Foramol sediment from the Golfe d'Arguin, Mauritania. **a** Coarse-fraction shows abundant fish remains indicating high biological productivity, and a dominance of the bivalve *Donax burnupi*. **b** Tropical gastropod *Persicula cingulata* demonstrates the warm-water conditions. **c**, **d**) Modern heterozoan sediment from the Gulf of California. **c** Red-algal-dominated sediment from mesotrophic section of gulf, **d** Bryomol sediment from eutrophic northern Gulf of California

settings. The bivalve *Crassatina* sp. and gastropods like *Prunum annulatum*, *Persicula cingulata*, and *Marginella sebastiani* demonstrate that tropical water temperatures prevail (Fig. 4b). The minor role of red algae has been explained by a lack of hard substrate (Milliman 1977) and by the low light transparency (J. Michel, G. Mateu-Vicens, H. Westphal, 2010, Eutrophic tropical carbonate grain associations—the Golfe d'Arguin, Mauritania, submitted; J. Michel, H. Westphal, R. von Cosel, 2010, The mollusk fauna of soft sediments from the tropical, upwelling-influenced shelf of Mauritania (NW Africa), submitted).

Yucatan Shelf off Mexico

On the Yucatan Shelf (20–23°N) in the Gulf of Mexico, photozoan carbonates (reef buildups with *Porites* and *Acropora*) with well-developed coral reefs form in direct vicinity of heterozoan tropical carbonates (Logan 1969; Logan et al. 1969). Topographical upwelling in the east of the Yucatan Shelf is thought to be responsible for the suppression of photozoan carbonates on the eastern shelf. The Yucatan Shelf receives no terrigenous input, because no fresh water reaches the coastline of the highly karstified hinterland (Merino 1997). Sea surface temperatures average between 24 and 30°C, but cool, nutrient-rich upwelling waters (17–18°C) from the Yucatan channel periodically (in spring and early summer) reach the eastern side of the shelf (Merino 1997), leading to temporarily increased primary production on the order of 1 mg * m^{-3} Chl-a, which corresponds to meso-/eutrophic conditions (Martínez-López and Zavala-Hidalgo 2009). While the waters warm up on the shelf, the trophic level remains elevated. The resulting carbonate sediment is characterized by foramol composition. Down to water depths of 50–80 m the sediment consists of bivalves, gastropods, *Halimeda* plates, and red algal fragments, plus peneroplids and miliolids (Logan et al. 1969). No information is available on the sediment composition in the easternmost part of the Yucatan Shelf where the upwelling water masses hit the shelf. Aragonite mud, an important component of classical tropical carbonates, is restricted to the western Yucatan Shelf where coral reefs prevail (Hoskin 1963). Because the Yucatan Shelf is not protected by a continuous reef barrier, the sedimentary system is strongly influenced by high water energies caused by currents and storms.

Nicaragua Rise

On the Nicaragua Rise, carbonate accumulation on the shallow platforms of the Nicaragua Rise has not kept pace with Holocene sea-level rise, despite a tropical location remote from terrigenous sedimentation (Hallock et al. 1988). Topographical upwelling causes elevated nutrient levels on the western Nicaragua Rise (Roberts and Murray 1983; Hine et al. 1987; Hallock et al. 1988; Triffleman et al. 1992). The decreasing trophic resources from west to east are accompanied by a gradient in the association of carbonate producers (Hallock et al. 1988). On the western platforms of the Nicaragua Rise, trophic resources exceed levels favouring coral-reef development, and sponge-algal communities predominate (cf. Hallock and Schlager 1986). Carbonate sediment on the western platforms is produced by calcareous green algae such as *Halimeda* (Hine et al. 1987), which makes the western Nicaragua Rise a chloralgal tropical carbonate system characterized by an absence of corals. This is in contrast to the well-developed coral reefs along the Jamaican coast on the eastern Nicaragua Rise.

West Florida Shelf

On the West Florida Shelf (26–28°N), high fluvial input of fine-grained terrigenous material raises nutrient levels (Gould and Steward 1956; Doyle 1986), while tropical water temperatures persist (20–30°C; Gorsline 1963). This results in a suppressed coral carbonate production, accompanied by high percentages of green algal-dominated carbonates. Hence, an impoverished photozoan carbonate community persists under elevated trophic resources, but tropical sea surface temperatures.

Gulf of California, Mexico

Located in a low-latitude setting (23° to 30°N), the Gulf of California is characterized by warm-temperate conditions (minimum monthly water temperatures in the south of 19°C and in the north 10°C; Alvarez-Borrego 1983) and encompasses nutrient regimes from oligo-mesotrophic in the south to eutrophic in the north (Alvarez-Borrego and Lara-Lara 1991; Halfar et al. 2006). Along with increasing nutrients, depth of light penetration decreases. Accordingly, carbonate production ranges from coral- dominated shallow-water areas in the south to extensive rhodolith-dominated, inner shelf carbonate production in the central gulf, and to molluscan-bryozoan inner- to outer-shelf environments in the northern gulf (Fig. 4b, c; Halfar et al. 2006). With respect to modern rhodolith-dominated carbonates, the Gulf of California is one of the best-studied regions in the world (Steller and Foster 1995; Hetzinger et al. 2006). While zooxanthellate corals are present throughout the gulf, they form a reef-like structure only in the southernmost oligotrophic setting (Riegl et al. 2007). Other photozoan carbonate producers such as green algae are not found in the sediment, even though sparse living plants have been observed in the southern gulf (Halfar et al. 2006). In contrast to classical coralgal sediments, the carbonates and coral structures from the Gulf of California are poorly

cemented (Halfar et al. 2001). While the Gulf of California carbonates were calibrated against in situ measured nutrient and temperature time series in order to highlight the influence of increasing trophic conditions along a gradient of carbonate systems, the accompanying trend of decreasing temperatures complicated the interpretation.

Water energy

Water energy also has a suppressing effect on zooxanthellate reefs. In continuously or sporadically high-energy settings, other photozoan organisms (red algae, stromatolites) replace the typical tropical coralgal association.

Fernando de Noronha (Brazil)

The island (3°25′S) off the Brazilian coast is exposed to extremely high water energy related to tidal forces (Jindrich 1983). Because of unrestricted wave fetch, ocean swell creates heavy surf with a spring tide range of 255 cm (Jindrich 1983). The carbonate framework here is composed of calcareous algae (*Neogoniolithon*, *Sporolithon*) and vermetid gastropods (*Dendropoma*) complemented by other encrusters such as *Homotrema*, bryozoans, serpulids and barnacles (Branner 1904; Kempf and Laborel 1968; Laborel 1969; Jindrich 1983). *Halimeda* and hermatypic corals locally form dense structures but no true reefs (Jindrich 1983). In addition to the high tidal energy, the geographical isolation could play a role in inhibiting coral reef development by hindering larval dispersal. Early cementation by aragonite and HMC is pervasive and is interpreted to be a result of the high tidal energy (Jindrich 1983).

Salinity

Lees and Buller (1972) already pointed out the role of salinity for the development of the different carbonate grain associations. The optimum range for chlorozoan associations is roughly at 31–40‰; outside this range the community shifts towards an association of euryhaline opportunists.

Persian Gulf, Red Sea, Tunisian Shelf

The Persian Gulf is characterized by high seasonal temperature variations, high salinity, low clarity and nutrient-poor water. Salinity is a major controlling factor determining the composition of carbonate-producing biota. Persian Gulf corals have partly adjusted to this high variability and can tolerate higher salinity and temperature changes. In areas with >50‰ salinity, corals, calcareous algae and echinoderms and most of the foraminifers are absent (Poiriez et al. 2010; Purser 1973).

In contrast, in the Red Sea, salinities are also elevated (40–46‰; Piller and Rasser 1996); however, green algae are present, albeit in rather low abundance and coral reefs are developed (Piller and Mansour 1990; Gabrié and Montaggioni 1982). Green algae are also abundant components in the sediments on the hypersaline Tunisian Shelf (Burollet 1981) and the Tunisian Ghar El Melh lagoon that shows strongly elevated salinities (44‰ in summer with extreme values of up to 54‰; Shili et al. 2002). The relationship between elevated salinities and the occurrence of calcareous green algae thus is not clear.

Shark Bay, W-Australia

Shark Bay shows a strong salinity gradient from normal-salinity tropical waters to extremely hypersaline waters in Hamelin Pool (56–65‰; Logan 1961). The high salinities in Hamelin Pool lead to a strong restriction of multicellular benthic organisms (mainly the zooxanthellate bivalve *Fragum erugatum*; Berry and Playford 1997), thus giving way to the formation of algal mat-mediated stromatolites. These stromatolites with their living cyanobacterial surface were the first modern stromatolites described (Logan 1961). It is now well known that stromatolites also prosper in normal-marine salinities where competing benthos is restricted, e.g., by mechanical stress as for the Bahamian stromatolites that grow in high-energy, ooid-loaded waters (Reid et al. 1995).

Oscillating oceanographic conditions

Tropical East Pacific

The tropical East Pacific is a region of poor coral-reef development due to a shallow thermocline, internal wave oscillations, slightly reduced salinity in areas close to coastlines, and high seasonal turbidity (Dana 1975). The impoverished nature of eastern Pacific coral communities is most likely a result of temporal and spatial isolation from source areas of high diversity, and of frequent disturbances that are peculiar to this region (Glynn 1996). Specifically, coral-reef development is suppressed by sporadically occurring cold-water intrusions associated with a shallowing of the thermocline during El Nino events (Glynn 1994). In the Gulf of Chiriquí at the Costa Rican Pacific Coast, temperature changes related to thermocline variability reach some 7°C; changes that should be detrimental to hermatypic coral growth (Dana 1975). In fact, the 1982/83 El Nino event resulted in 95–99% mortality of the coral communities in Galapagos (0°32′S) and Cocos Islands (5°32′N), with recovery being slow (Glynn 1997). Instead, carbonate producers that are more tolerant to temperature changes, such as coralline red algae and barnacles,

have established flourishing communities, with barnacles (*Balanus tintinnabulum* and *Tetraclita* sp.) forming reef-like accumulations around Cocos Island (Glynn and Wellington 1983; Senn and Glasstetter 1989). Individual balanids reach sizes of 80 mm in height and form thick accumulations as a result of gregarious settlement. Coralline red algae stabilize the barnacle aggregations. Coralline algae are important ecosystem components in many areas of the Galapagos (Glynn and Wellington 1983) where they locally form rhodolith beds (Foster 2001).

A recently discussed factor adding to the impoverished nature of Eastern Pacific coral communities is the low pH and low aragonite saturation state of the seawater in this area (Manzello et al. 2008). This low pH is the consequence of upwelling mixing CO_2-enriched deep waters into the surface layers along the shallow thermocline (e.g., Manzello et al. 2008). It results in poor cementation of coral reef structures and may favour the high bioerosion rates previously reported for Eastern Tropical Pacific reefs (Eakin 1996). However, elevated nutrients in upwelled waters may also limit cementation and/or stimulate bioerosion (Manzello et al. 2008). Conditions leading to aragonite undersaturation are even more pronounced during recurring El Nino events that force enhanced upwelling of CO_2-rich deep water. Hence, tropical carbonate systems similar to the ones of the East Pacific might become more common globally with an expected increase in ocean acidification (De'ath et al. 2009).

Geographical situation

NE-Brazilian shelf

On the tropical Brazilian shelf between 0 and 15°S, carbonate sediments are dominated by *Halimeda* and ramiform red algae with subordinate encrusting red algae, rhodolites, bryozoans and large benthic foraminifers (*Amphistegina*, *Archaias*) (Milliman and Summerhayes 1975; Vicalvi and Milliman 1977; Carannante et al. 1988). Zooxanthellate corals are rare with a low diversity and a high degree of endemism (Spalding et al. 2001, p. 173).

Between 15 and 23°S, encrusting red algae and rhodoliths dominate. Here, zooxanthellate corals are entirely absent. While parts of the tropical Brazilian shelf are influenced by fluvial runoff, in the semiarid NE of Brazil, only little sediment load from the Amazon and San Francisco rivers reach the shelf, and the waters are clear, show temperatures of 26.5–28.5°C and normal salinity (Testa and Bosence 1999). These conditions would be expected to favour the development of typical tropical carbonates that in fact are largely absent here. The reason is thought to be an oceanographic blocking of the southward transport of coral planulae from the Caribbean to the Brazilian shelf by the low-salinity and high-sediment load plume of the Amazon river (Spalding et al. 2001, p. 173). Testa and Bosence (1999) suggest that additionally the extremely high water energy and the continuous movement of sediment counteracts benthic settling. Wilson (1986, 1988) has pointed out that low-diversity benthic communities are characteristic for strongly moving sediments and high water energy conditions.

Eastern Mediterranean

The oligotrophic (Patara et al. 2009) Eastern Mediterranean with its subtropical water temperatures (14–28°C) and salinites (>37‰; Morel 1971) largely lacks zooxanthellate coral reefs (the only zooxanthellate hermatypic coral is *Cladocora caespitosa*). Here, the absence of a tropical corridor is held responsible for the scantiness of tropical elements.

The formerly rich warm-water fauna of the Mediterranean, including zooxanthellate coral reefs, vanished during the Messinian salinity crisis. When the connection to the open ocean opened again at the straits of Gibraltar, new ecosystems established (Bouillon et al. 2004). Today, the Western Mediterranean is richer in marine species than the Eastern basin. One reason put forward is that the Eastern Mediterranean with its great tropical affinity is isolated from tropical species entering from Gibraltar by the temperate barrier of the Western Mediterranean (Bouillon et al. 2004). This assumption is corroborated by the observation that since the opening of the Suez Canal, tropical species invading from the Red Sea now thrive and expand in the Eastern Mediterranean (Bouillon et al. 2004).

Ancient heterozoan warm-water carbonates

An increasing number of ancient occurrences of heterozoan warm-water carbonates have been recognized lately; mostly from the Neogene of the Western Mediterranean (Brandano and Corda 2002; Pomar et al. 2002, 2004; see also Halfar and Mutti 2005), but also from the Mesozoic (Hornung et al. 2007). These occurrences are reminiscent of cool-water carbonates but have formed under warm-water conditions with increased trophic levels as evidenced by the predominance of nutrient-tolerant groups of calcareous organisms, supported in some cases by high amounts of suspension feeders and high rates of bioerosion. These examples demonstrate the potential importance of heterozoan warm-water carbonates throughout the Phanerozoic. However, the documented number of examples in the rock record is still limited. One reason might be that they have not yet been recognized as such. Most of the

described occurrences are of Neogene age, pointing to the fact that the older the rock, the more difficult it is to interpret carbonate rocks on the basis of modern analogues. For interpreting heterozoan carbonate deposits, it is crucial to separate the relative influence of different parameters such as temperature, trophic conditions and ocean chemistry, etc. (e.g., Pomar et al. 2005; Halfar et al. 2006). In the following, examples are presented that have been interpreted as tropical carbonates in spite of their heterozoan character, and the steering mechanisms for the biotic associations are discussed.

Changing trophic conditions

Upper Miocene, Balearic Islands

On the Balearic Islands, a foramol-rhodalgal carbonate ramp (Tortonian to lower Messinian; Fig. 5) is stratigraphically succeeded by a zooxanthellate coral reef (upper Messinian; Pomar 2001a). The ramp system is of tropical origin as suggested by larger foraminifers and the red algal association (Brandano et al. 2005; Mateu-Vicens et al. 2008). The transition from the ramp system to the rimmed reef platform thus is not driven by water temperature; rather, it reflects the transition from a humid to a more arid climate that is implied by paleoclimatic reconstructions (Pomar et al. 2004). The terrigenous input from the hinterland during the formation of the ramp had suppressed the development of a classical tropical reef system. When the terrigenous input was diminished by arid conditions, the zooxanthellate coral reef system could establish.

Mid to upper Miocene, Lazio-Abruzzi platform, Apennines

This Serravallian-Tortonian carbonate succession is a foramol carbonate ramp system. Taxonomic studies have shown that the red algae are clearly tropical (Brandano 2001; Brandano and Corda 2002). In addition, rare hermatypic corals have been found. The high density of suspension feeders and the intense bioerosion point to elevated trophic conditions. The increasing nutrient levels have been interpreted to reflect the development of a foredeep and the approach of the orogenic front of the Apennines.

Mid-Miocene, tropical Pacific Islands

In the Mid-Miocene, rhodolith-dominated facies with a thickness exceeding 100 m succeeds the Early Miocene coral-reef deposits over wide areas of the equatorial Pacific Islands (Bourrouilh-Le Jan and Hottinger 1988). Major carbonate components of these tropical rhodolite facies are *Halimeda* and larger foraminifers (Bourrouilh-Le Jan 1979). The facies change from hermatypic coral to rhodolite deposits is explained by a thinning of the uppermost oligotrophic layer related to equatorial climate cooling and sea-level fall, introducing elevated nutrient conditions to near-surface water masses (Bourrouilh-Le Jan and Hottinger 1988).

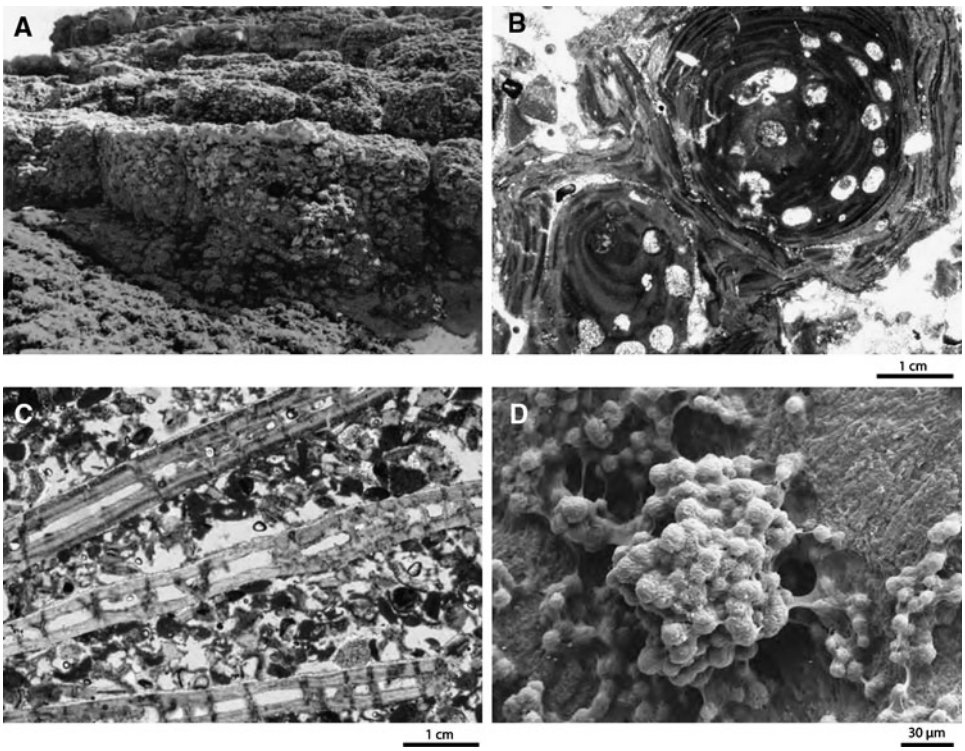

Fig. 5 Example from ancient heterozoan tropical carbonate ramp (lower Tortonian, Menorca). **a** Upper slope clinobeds composed of rhodolithic rudstone/floatstones with red algal grainstone matrix. Deposition is thought to have taken place close to the site of production in the deepest photic zone. Bed thickness is about 50 cm. **b** Red algae (*Sporolithon*) in upper slope rhodolithic rudstone clinobeds. **c** Larger benthic foraminifers (*Heterostegina*) indicative of subtropical to tropical conditions. **d** Cast of the trace of cyanobacterium *Fasciculus rogus* tentatively indicating elevated trophic conditions

Mid-Miocene, Pannonian Basin, Hungary

These rhodolith-dominated sediments have originally been interpreted as cool-water carbonates (Randazzo et al. 1999). However, rare *Porites* patch reefs demonstrate that the sediment formed under warm-water conditions (Halfar et al. 2000). Elevated trophic conditions are thought to have suppressed the flourishing of classical coral reefs. The origin of the nutrients has yet to be determined.

Early to late Miocene, SE-Asia

SE Asia has the most extensive and complete record of equatorial carbonates spanning the last 20 My (Burdigalian-early Tortonian; Wilson 2008). Declining SE Asian coral-reef facies were replaced in the late Early Miocene by large benthic foraminiferal biofacies with abundant coralline red algae (Wilson 2002). This facies is especially abundant in areas of terrestrial runoff or upwelling, with an indication that nutrients (high oligotrophy to mesotrophy rather than eutrophy) may have influenced Cenozoic development of this biofacies (Wilson and Vecsei 2005). Nutrient upwelling in SE Asia is a result of oceanic ventilation with enhanced thermohaline circulation and narrowing of oceanic gateways due to tectonic movement in the Indo-Pacific. In addition, seasonal runoff increased through initiation and/or intensification of the monsoons (Fulthorpe and Schlanger 1989; Wilson 2008).

Upper Cretaceous, NW Sardinia, Southern Appenines and Apulia

In large parts of Italy, tropical foramol sediments of Upper Cretaceous age crop out (Carannante et al. 1995, 1997; Simone et al. 2003). In this time interval, a strong increase in molluscs (most markedly in rudists) and red algae took place. The rudists replaced corals as dominant reef-building organisms. Other common carbonate-secreting organisms include bryozoans and benthic foraminifers whereas green algae disappear. At the same time, the amount non-skeletal components and aragonite cements decreases. These changes are interpreted to imply that the sediments have formed in deeper, darker, and more eutrophic conditions as the underlying typical tropical coral-bearing carbonates. However, as Pomar et al. (2005) pointed out, the Cretaceous corals flourished in deeper water than their modern equivalents, questioning the water-depth interpretation. Carannante et al. (1995) demonstrate that the extensive development of foramol associations in the tropical-subtropical seas of the Upper Cretaceous point to increased trophic conditions. High nutrient levels favour low-diversity associations of heterotrophic suspension feeders such as rudists (Scott 1995). In addition, in contrast to corals, the heterotrophic rudists were able to occupy mobile substrates (Pomar et al. 2005).

Upper Cretaceous, Northern Spain

The Upper Santonian to Lower Campanian *Lacazina* limestones consist of a foramol association (whereby the molluscs are dominated by bivalves with only subordinate rudists) that has been deposited under warm-water elevated trophic conditions (Gischler et al. 1994). Elevated nutrient levels caused by terrigenous input, possibly in concert with upwelling, have suppressed reef growth and the formation of a chlorozoan association. This is supported by the dominance of miliolid foraminifers that are known to replace other benthic foraminifers under high nutrient conditions (Hallock 1985).

Lower Cretaceous, Northern Spain

The lowermost Aptian in the central part of the Northern Cantabrian Basin is represented by a carbonate ramp depositional system (Wilmsen 2005). The facies is of mixed chloralgal-foramol character with a strongly dominant foramol association. Hermatypic corals are absent, and the biofacies is dominated by heterotrophic organisms such as oysters, brachiopods, echinoids, solitary corals. A strong terrigenous input under wet-subtropical climate is held responsible for high-nutrient warm-water conditions (Wilmsen 2005). The voluminous fluvial input is manifested in abundant siliciclastic grains and plant debris. Thus, the heterozoan carbonate facies was controlled by elevated nutrient levels rather than temperature (Wilmsen 2005).

Upper Triassic, NW Tethys

In the Carnian of the NW Tethys, a demise of coral reef–rimmed platforms was followed by the development of carbonate ramps, which were then again succeeded by rimmed reef platforms. This non-reefal interval has been interpreted to be related to a pronounced increase in precipitation, the so-called Carnian Pluvial Event (Simms and Ruffell 1989; Keim et al. 2001; Rigo et al. 2007; Hornung et al. 2007). Climate warming in the mega-monsoonal Triassic climate has intensified the hydrologic cycle and increased humidity (e.g., Parrish 1999; Wortmann and Weissert 2000) resulting in enhanced freshwater runoff that led to higher nutrient levels and a lowered salinity in the ocean. This nutrification of and increased sediment input into sea surface waters could have had negative consequences for Upper Triassic shallow-marine coral reef builders, which lived in assumed symbiosis with zooxanthellate algae (Stanley and Swart 1995; Kiessling 2002). The increased abundance of epibenthic suspension feeders

suggests increased nutrient supply (Keim et al. 2001). Coevally, elevated nutrient supply advanced growth of fixosessile microbes and stimulated planktonic blooms. This leads to reduced water transparency, destabilisation of coral symbiosis, enhanced by increased bio-erosion (Keim et al. 2001). The dominance of megalodonts places this example in the foramol grain association.

Other examples of heterozoan tropical carbonates from Earth history that have been related to elevated trophic conditions include the middle to upper Permian shelves of Pangaea (Beauchamp and Desrochers 1997; Weidlich 2002) and some intervals of the Silurian of Gotland (Jeppsson 1990; Kershaw 1993; Bickert et al. 1997).

Changing ocean chemistry

The expansion of shallow-water aragonite factories in the Late Oligocene-Early Miocene (Budd 2000) has been interpreted to reflect declining atmospheric CO_2 concentrations to Neogene levels (Pearson and Palmer 2000). Scleractinian coral reef frameworks show a pronounced peak in abundance in the Late Miocene when CO_2 reached preindustrial concentrations (Perrin 2002; Pomar and Hallock 2007). Ocean chemistry appears to be a major determinant of the modes of calcification and shell mineralogies preferably precipitated by photozoans (Hallock 1996, 2005; Stanley and Hardie 1998). Observations in the modern world imply that increasing atmospheric pCO_2 acts on marine carbonate secreting biota by reducing the carbonate saturation (in particular the aragonite saturation) in seawater, thus leading to reduced calcification of the skeletons (Opdyke and Wilkinson 1993; Kleypas et al. 1999; Kleypas and Langdon 2001; Hallock 2005; De'ath et al. 2009).

In addition, the concentration of Ca^{2+} and the Mg/Ca ratios significantly influence carbonate-secreting organisms. The combination of high Ca^{2+} concentrations with low Mg/Ca ratios seem to have a stronger influence on the dominance of calcite precipitation over aragonite than high atmospheric CO_2 concentrations such as in the Cretaceous (Stanley and Hardie 1998; Ries 2006).

Evolutionary change

During Earth history, a wide range of organisms has filled the ecological niche of shallow-water reefs (e.g., Pomar and Hallock 2008; Kiessling 2005). Among those organisms were phototrophic as well as heterotrophic and symbiotic framework builders. In addition, several groups of carbonate-secreting organisms have migrated between different ecological niches and thus indicate different ecological conditions in different time intervals. Due to biological evolution, the deeper in time, the more difficult it is to interpret the paleoecology of carbonate deposits.

But even in the younger Earth history, interpretations of facies are far from straightforward. Zooxanthellate corals expanded into shallow-water habitats in the Late Miocene (Pomar and Hallock 2008). Global cooling in combination with changing seawater chemistry that supported hypercalcification of aragonitic corals (cf. Ries et al. 2006) is suggested to have led to the migration of the corals in the shallow euphotic zone (Pomar and Hallock 2007). However, the coevolution of corals and *Symbiodinium* zooxanthellae appears to have played an important role for the migration into shallow waters. Previously, the limited capacity of zooxanthellate corals to thrive in high-light conditions is thought to have prevented them from forming a wave-resistant reef (Pomar and Hallock 2007, 2008). This promoted the dominance of heterozoan assemblages in oligotrophic tropical waters, e.g., in the Upper Oligocene sediments of Malta that form a carbonate ramp dominated by coralline algae (Brandano et al. 2009). Similarly, in SE Asia, Paleogene carbonates were dominated by coralline algae and benthic foraminifers with only scarce corals despite tropical latitudes (Wilson and Rosen 1998; Wilson 2008).

Other steering mechanisms

Differentiating the various steering mechanisms is difficult in the geological past, and it becomes more difficult the less is known about the oceanography of the time slice, and the deeper in time the carbonate system has formed. Nevertheless, there are reports of other controlling factors than the aforementioned trophic conditions, CO_2 and Ca^{2+} concentrations, Mg/Ca ratio, and evolutionary change, leading to the development of heterozoan warm-water carbonate facies. These include water energy (e.g., those Cretaceous rudists that were adapted to high-water energies: Simone et al. 2003; the high-energy rhodolite platforms of the Mio-Pliocene Pacific: Bourrouilh-Le Jan 1979), and salinity (among many other examples the stromatolites and serpulid or sabellarid reefs of the Messinian in the Western Mediterranean, Esteban 1979).

Heterozoan warm-water carbonates—more abundant in Earth history?

In the modern world, heterozoan warm-water carbonates are restricted to a variety of settings that appear disturbed compared to the tropical oligotrophic coralgal carbonates we regard as typical for modern tropical carbonate depositional settings. However, during large intervals of Earth history, heterozoan warm-water carbonates might have been the rule rather than the exception. During greenhouse periods, the hydrological cycle was strongly enforced and thus has led to increased evaporation, precipitation, erosion, fresh-water and sediment influx in warm ocean

waters. It seems likely that during such periods, high-nutrient, heterotrophic dominated carbonates have been more abundant than in our present-day icehouse world with its oceanic deserts in the tropics. It might be speculated that as a result of current climate warming, such high-nutrient settings will expand. Thus, the examples presented here might serve as models for future developments—with possible consequences, e.g., on coastal protection where coral reefs disappear. Similar, for better predicting the effect of future increasing pCO_2 and ocean acidification, modern heterozoan carbonate-depositional systems offer important information.

As Pomar and Kendall (2007) have pointed out, study of the various types of carbonate depositional systems in the geological record will demonstrate the wide variety of environmental conditions and ecosystem reactions and finally lead to deemphasizing the Holocene uniformitarian approach. The continuum approach of Wright and Burgess (2005) offers a first basis for filling the gaps between the classical carbonate depositional realms.

Recognizing ancient heterotrophic warm-water tropical carbonates

Recognizing heterozoan warm-water carbonates is a prerequisite for reaching reliable interpretations of heterozoan carbonate deposits. As pointed out earlier and illustrated with the examples given, carbonate grain associations are inadequate for this task. Other tools are required to support a well-founded interpretation. These approaches are listed in Table 1.

Conclusions

A wide range of parameters can suppress coralgal carbonates in warm-water settings; this includes elevated trophic conditions but also high water energies, geographical isolation, instability of the oceanographic conditions, and many others. The current models of carbonate depositional realms are based on an actualistic approach—from this actualistic point of view, the widespread heterozoan associations in the past are atypical. However from the perspective of other intervals of Earth history, heterozoan warm-water carbonates were the rule rather than the exception.

As already pointed out by the authors elsewhere, more calibration studies are needed to define the mulitparameter space of carbonate grain associations (e.g., nutrients-temperature, Gulf of California: Halfar et al. 2004; Golfe d'Arguin: (J. Michel, G. Mateu-Vicens, H. Westphal, 2010, Eutrophic tropical carbonate grain associations—the Golfe d'Arguin, Mauritania, submitted; J. Michel, H. Westphal,

Table 1 Proxies of environmental conditions of carbonate depositional systems

Proxy/indicator	Comment	Examples
Taxonomy	The higher the level of taxonomic determination, the more reliable the interpretation of the environmental conditions	Aguirre et al. (2000)
Red algae		Brandano et al. (2009)
Larger foraminifers		Pomar et al. (2004)
Palynomorphs		
Geochemistry	For reconstructing water temperature and paleoproductivity, depth habitat of benthic and planktonic organisms has to be considered	Kroopnick (1985)
Oxygen and carbon isotopes, phosphate concentrations and trace elements of diagenetically pristine benthic and planktonic organisms		Lea and Boyle (1990, 1993)
Nitrogen isotopes of fish scales	Trace elements in benthic foraminifers help to assess phytoplankton productivity, Ba/Ca ratio is indicator for upwelling (but also of riverine input), Cd/Ca ratio and phosphate content are indicators for trophic conditions	Mutti and Hallock (2003) Struck et al. (2004) von Breymann et al. (1992)
Carbonate grain associations	1–20% photozoan components in a heterozoan sediment could point to warm temperatures and high nutrient conditions	Carannante et al. (1988)
Photozoan-heterozoan transition (cf. Fig. 3)		Halfar et al. (2004)
Presence of planktic shells	Planktonic organisms can be indicators of upwelling (e.g., diatoms, radiolarians)	
Paleoceanographic context	Indications of upwelling, regional current patterns, fluvial influx from hinterland, dust input	Parrish et al. (2001)
Phosphate hardgrounds		Philip and Gari (2005)
Current erosion, ripples		Stanton (2006)
Siliciclastic grains (clay, silt)		

R. von Cosel, 2010, The mollusk fauna of soft sediments from the tropical, upwelling-influenced shelf of Mauritania (NW Africa), submitted). As detailed earlier, useful tools for distinguishing between extratropical carbonates and warm-water heterozoan carbonates include taxonomic study, oceanographic context, and geochemical proxies. Study of such examples will extend the understanding of such ecosystems, allow for calibrating further proxies, and it will help to better predict future changes in the oceans.

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